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COMIA, A SEED PLANT POSSIBLY OF PELTASPERMOUS AFFINITY: A BRIEF REVIEW OF THE GENUS AND DESCRIPTION OF TWO NEW SPECIES FROM THE EARLY PERMIAN (ARTINSKIAN) OF TEXAS, *C. GREGGII* SP. NOV. AND *C. CRADDOCKII* SP. NOV.

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Comia is a widespread foliage morphogenus of probable seed plant affinity primarily known from rocks of Late Permian age, in the Angaran and Cathaysian paleobiogeographic regions. It also occurs in the Early Permian of the western Euramerican equatorial paleobiogeographic region. Vegetative features and consistent association with peltaspermous reproductive organs suggest affinity with the Peltaspermales. New material from north-central Texas allows two new species to be attributed to this genus, *Comia greggii* and *Comia craddockii*. Both species are uncommon elements of the Early Permian (Leonardian-Artinskian) flora. They exhibit a diagnostic form of venation typical of *Comia* and allied forms, in which the tertiary veins form fascicles and interfascicular groups. Ultimate veins extend from their insertion point to the laminar margin, usually with one dichotomy. They neither anastomose nor terminate in blind endings. In gross architecture, *C. craddockii* is once pinnate. The morphology of the frond of *C. greggii* is not known. The much wider, more finely veined laminae of *C. greggii* are clearly distinguishable from the narrow pinnules with coarser venation of *C. craddockii*. (Russian and Chinese translations of this abstract are available in the online edition of *International Journal of Plant Sciences*.)

Keywords: paleobotany, Paleozoic, Clear Fork Formation, *Comia*, peltasperm.

Online enhancements: Chinese and Russian abstracts.

Introduction

The flora of the Early Permian of equatorial Pangea has emerged slowly over more than 100 years (White 1892, 1912). Texas, in particular, has been the source of many Early Permian genera that later appeared as major elements in Late Permian floras from Angara and Cathaysia, particularly among the gigantopterids (Mamay 1960, 1986, 1988, 1989; Mamay et al. 1988), peltasperms (Kerp and Fichter 1985; Broutin et al. 1998; Berthelin 2002; Berthelin et al. 2003), and conifers (DiMichele et al. 2004; Looy 2007). Many genera presently considered to be of uncertain affinity in fact may be peltasperms (Naugolnykh 1999; DiMichele et al. 2005), a group that may have undergone a major radiation in seasonally dry areas of the tropics beginning in the latest Carboniferous or earliest Permian.

The Early Permian red beds of north-central Texas have yielded a rich flora predominantly consisting of compression/impression foliar elements. Rare specimens are permineralized, preserved by replacement or as casts, and show exquisite details of the cellular structure both of the epidermal layer and internal structures.

Recent discoveries in these rocks (fig. 1) have revealed an abundance of compression/impression foliage remains assignable to the genera *Comia* (Zalessky 1934) and *Auritifolia* (Chaney et al. 2009). The biologic relationship between these two genera at or below the familial level is not known with certainty; however, we believe both to be peltasperms, based on their common co-occurrence with *Sandrewia* (*Autunia*)–like peltate reproductive structures in assemblages where callipterids are rare or absent. *Comia* and *Auritifolia* have strong similarities in the organization of their laminar veins while being distinct in the fine details and overall gross morphology of the leaf. We herein refer to these two genera as "comioid." Comioids merit particular attention for two reasons. First, they have a cosmopolitan distribution in the Angaran (north-central Asia), Cathaysian (southeastern China), and Euramerican (western Europe and North America) paleobiogeographic regions and also occur in floras with mixed Gondwanan (Southern Hemisphere temperate) and Euramerican elements. Second, the occurrence of comioids in north-central Texas is the earliest yet reported for the group.

The presence of *Comia* in north-central Texas was first recognized by Meyen (1970) on the basis of a specimen (USNM 41778) published as "*Callipteris* cf. *C. adzvensis* Zalessky" by Read and Mamay (1964). Before Meyen's publication, *Comia* had been reported only from the Late Permian of the Angaran and Cathaysian floral realms.

Comia is one of more than 160 fossil plant generic names proposed by M. D. Zalessky in a series of ~60 publications that appeared between 1903 and 1948 (Andrews 1970). Zalessky's papers (1918, 1927) discuss fossil plant collections from many Paleozoic fossiliferous areas in Angaraland, and he, more than any other single person, is largely responsible for the pre-

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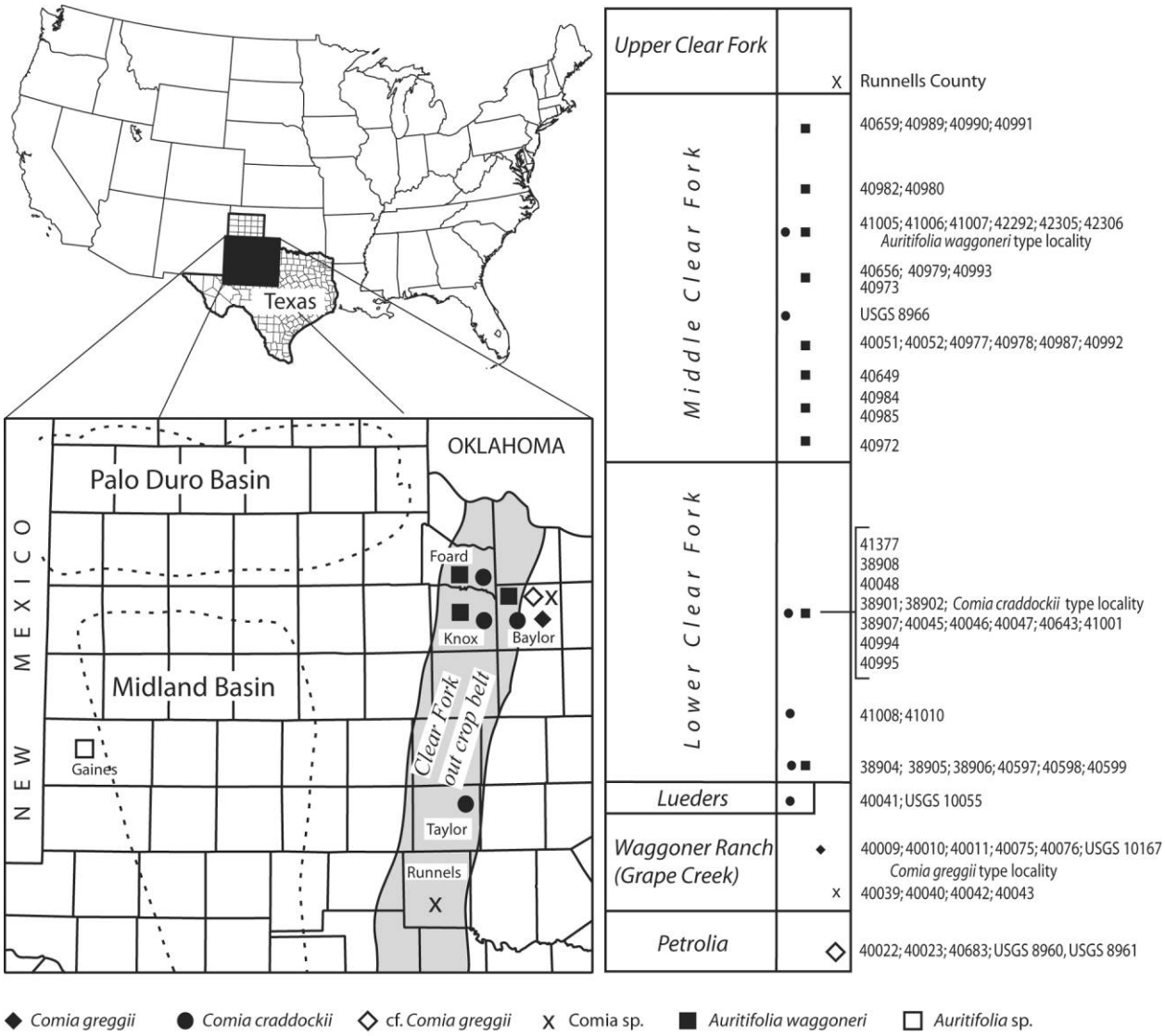

Fig. 1 Geographic setting and geologic distribution of *Comia*. Map of the United States with study area indicated by black box. Regional geologic basins of north-central and west Texas indicated. Outcrop belt of Clear Fork Group shaded with gray. Named counties are those in which a comioid has been identified. Symbols indicate occurrence of a particular comioid in that county. A generalized stratigraphic column shows comioid distribution and localities from which comioids have been collected.

1950s documentation of the Angara flora and for stimulating succeeding Russian paleobotanists to investigate it further. Later, a history of Angaran paleobotany was published by Meyen (1982).

Even though much of Zalessky's material was destroyed during World War II (Meyen 1982), *Comia* is sufficiently distinctive to have merited general acceptance as a valid genus and has been found in several far-flung Eurasian areas. Before the present discoveries in North America, ~30 specific names have been proposed in Russian and Chinese publications (apps. A, C).

Nomenclatural History of Comia

Zalessky (1934) described *Comia pereborensis* (fig. 2), a single species of a new genus, based on a small suite of pteridophylls from Upper Permian strata in the Pechora Basin in northeastern Europe. The fronds of this species are large and pinnately compound, with linear-lingulate pinnae. Zalessky noted a resemblance of this foliage to *Taeniopteris* leaves, speculating that if it is not marattiaceous, *Comia* could represent a seed fern with marattioid foliage. However, the venation of *Comia* clearly separates it from other Paleozoic pteridophylls. Lateral veins are thin, simple or dichotomous, and arise from a thick midvein in such a manner as to form fascicles at regular, widely spaced intervals. Between the fascicles, single simple or dichotomous veins arise independently. Zalessky's (1934) two illustrations, his figures 44 and 45, clearly show this fasciculate arrangement and further indicate an absence of anastomoses between the closely spaced ultimate veins, all the vein endings terminating at the laminar margin.

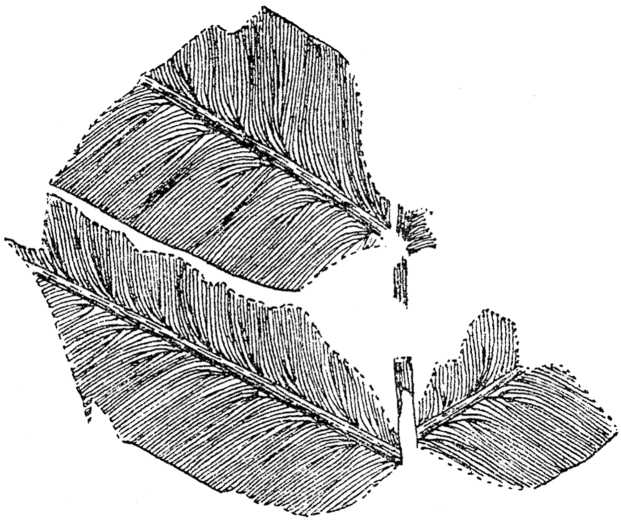

Fig. 2 Zalessky's (1934) line drawing of the lectotype of the genotypic species of *Comia*. Specimen was destroyed in World War II. Scale is not known. Fascicular-interfascicular arrangement of the tertiary veins is clearly represented.

The next report of *Comia* appeared when Neuburg (1948) presented a concise diagnostic condensation of Zalessky's lengthy description and described "*C.? primitiva*" as a new species from the Upper Permian of the Kuznets Basin. Several other Russian investigators subsequently described additional Angaran species of *Comia*; *Comia latiloba* and *Comia congermana* were described by Burago (1983) from Upper Permian strata of the Primorya Region in eastern Russia (what was then the U.S.S.R.). Earlier, Rasskazova (1963) published a chart comparing the then-known 14 Russian species of *Comia* (app. C).

Comia was first reported in Upper Permian beds of northeast China by Huang (1966), who named *Comia yichuensis* in a bilingual article (Russian and Chinese). Huang later named five additional species (Huang 1977) and included a chart comparing 10 *Comia* species, omitting some of the then-known Russian taxa (app. C). Additionally, Huang (1977) provided a chart highlighting the differences between the genera *Comia*, *Fascipteris*, and *Validopteris* (table 1). *Comia contracta* and *Comia minor*, reported by Liu and Yao (1996) from the Upper Permian of northwest China, brought the Chinese complement of the genus to ~13 species that, combined with the names originating from Russia, bring the total number of specific names published for *Comia* to more than 30.

Aside from Zalessky's original French article, all other descriptions are either in Russian or Chinese. The highly technical vocabulary creates problems for many of the available translators, with the result that linguistic nuances impede satisfactory translation. Further, some of the names have been erected on the basis of small or single fragments, many of which are poorly preserved and are accompanied by illustrations that do not reveal critical characteristics. These factors and the logistic obstacles to actual examination of original specimens have discouraged us from including the Texas specimens within the circumscriptions of any previously named species of *Comia*. On the basis of available documentation, then, we recognize two new species of *Comia*, described herewith. For the benefit of other researchers who may wish to explore further the taxonomy of *Comia*, we have included in appendix A a briefly annotated list of the specific names encountered in our study of the genus.

In North America, a specimen (USNM 41778) illustrated by Read and Mamay (1964), with what we now recognize as "comioid" venation, was misidentified as "*Callipteris* cf. *C. adzvensis* Zalessky," an Angaran species. The error was recognized by the late S. V. Meyen, who advised Mamay (personal communication, Nov. 28, 1964) of the correct generic identity of the specimen and later published his correction (Meyen 1970). *Comia* sp. reported by DiMichele et al. (2000) is now reclassified in the genus *Auritifolia* sp. Chaney et al. 2009. Weber (2007) reported *Comia* in the Permian of the state of Puebla, Mexico, on a Web site with a photograph and a brief description.

Geographic and Geologic Setting

Comia in North America occurs in surface outcrops in Baylor, King, Foard, and Taylor counties of north-central Texas and in Mexico, as mentioned above. The nonmarine stratigraphy in north-central Texas was revised by Hentz (1988) and Hentz and Brown (1987). Before this revision, the paleontological material recovered from these rocks was indicated as coming from formations whose names now refer to predominately marine strata. All of the North American localities are Leonardian (Artinskian, Cisuralian), Early Permian in age (fig. 1). In north-central Texas, these plants occur in channel-fill sediments of coastal-plain environments ranging from riparian to pond margin. Lithologies vary from accretion-bedded sandstones

Table 1

Comparison of Genera with Comioid or Comioid-Like Venation

	Comia	*Fascipteris*	*Validopteris*
Frond	Once pinnately compound	Once or twice pinnately compound	Once or twice pinnately compound
Pinnules	Large and wide	Small, narrow, long-linear, twice pinnate	Small, narrow, long-linear, twice pinnate
Pinnule base	Wide bases on axis or decurrent on axis, with adjacent vein	Contracted base or wide base on axis, without adjacent vein	Contracted base or normal base on axis, without adjacent vein
Veins	Lateral veins forming fascicles, with interfasciculary veins	Lateral veins forming fascicles, with no interfasciculary veins	Lateral veins forming fascicles, with interfasciculary veins

Note. *Comia*, *Fascipteris*, and *Validopteris* all have fasciculate venation. Terminology modified to reflect that used in this article. It may be difficult, on the basis of venation alone, to distinguish *Validopteris* from *Comia* if specimens are fragmentary. *Fascipteris* lacks the interfascicular veins typical of *Comia*. Source: after Huang (1977).

deposited in active channels to finely laminated claystones deposited in standing water (app. B).

Terminology

The fasciculate architecture of the comioid venation invites a novel terminology. Previously there has not been a uniform terminology to describe the comioid venation pattern, and the terminology from other languages does not translate well into meaningful English. We suggest what we believe to be a clear terminology based on the following understanding of the comioid venation pattern. So far as is determinable, all veins appear identical in size and aspect at their termini at the foliar margin. They obviously entail different orders of venation, however, because in addition to the midvein there is a dominant vein central to each fascicle (fig. 3). We assign these dominant veins to secondary rank, with all other veins regarded as tertiary rank. The lateral members of a fascicle are clearly tertiary; several of these may arise from each secondary vein at close intervals, usually dichotomize a short distance thereafter, and may undergo a second dichotomy before terminating at the foliar margin. With the departure of each successive tertiary vein, the parent secondary decreases in thickness so that it eventually loses its identity as a dominant vein about two-thirds or three-fourths of the distance to the margin. The small lateral veins that also originate directly from the primary vein (midrib) likewise usually dichotomize, and throughout their length are equal in thickness to, and are otherwise indistinguishable from, the fascicular tertiary veins. These veins are here termed interfascicular tertiary veins, a terminology more descriptive than that of Huang (1977), whose Chinese term translates to "assist" or "subsidiary" veins.

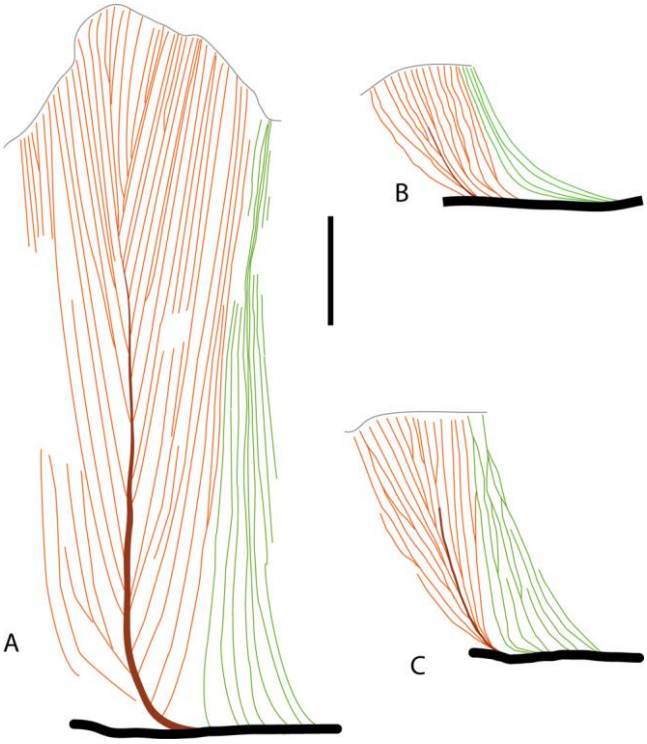

Fig. 3 Line drawings of fascicular-interfascicular complex of secondary and tertiary veins of *Comia* and *Auritifolia*; scale bar = 1 cm. Vein colors reflect vein designations: black = first-order vein (midrib); brown = second-order vein; reddish brown = third-order fascicular veins; green = third-order interfascicular veins. *A*, *Comia greggii* n. sp., paratype USNM 528609. Third-order veins represent what was observable. Termination prior to the margin reflects poor preservation; otherwise, all veins would terminate at the margin. *B*, *Comia craddockii* n. sp., holotype USNM 508138. Third-order veins represent what is observable; all veins terminate at the margin. *C*, *Auritifolia waggoneri*, USNM 528206. Third-order veins represent what is observable; anastomoses and blind endings are not artifacts of preservation.

Systematics

Division—Tracheophyta

Class—Spermatopsida

Order—Peltaspermales

Family—Incertae sedis

Zalessky's (1934) original description of *Comia pereborensis* does not include a formal diagnosis but describes *Comia* as a once-pinnate frond with pinnules having three orders of venation (fig. 2), the second order directly giving rise, on both sides, to third-order veins forming a fascicle, with individual fascicles separated one from the other by veins of third-order weight (interfascicular veins) arising directly from the first-order midvein; tertiary veins regardless of their origin may or may not dichotomize but do not anastomose or terminate short of the laminar margin in blind endings. Subsequent authors (cited elsewhere in this article) have come to refer to this type of venation as comioid. It is in this sense that we herein recognize this genus and the species referred to it.

Comia greggii *Mamay, Chaney & DiMichele sp. nov. (Figs. 4–7)*

Specific diagnosis. Pinnae large (20–30 cm long, to ~16 cm wide), margins shallowly crenate with sinuses ~15 mm apart. Venation three-ordered, open. Midvein moderately stout (~8 mm wide), with parallel, mostly weak surface striations. Secondary veins form alternate to subopposite fascicles at regular intervals of 14–16 mm, each distinguished by a strong, median secondary vein inserted at a widely acute angle and following a nearly perpendicular course. Thin tertiary veins arise from secondary veins at close (2–4 mm) intervals and narrow angles (5°–10°), tertiary veins dichotomizing sparsely. Several (6–10) thin interfascicular tertiary veins arise directly from the midvein between successive secondary veins and dichotomize sparsely; all ultimate veins end at the foliar margin in a concentration of ~15 per cm.

Holotype. USNM 528611 (fig. 4*A*).

Type locality. USNM locality 40076.

Paratypes. USNM 528609 (fig. 4*B*), USNM 528459 (fig. 5), both from USNM locality 40076; USNM 530888, USNM 536419, both from USNM locality 40010.

Stratigraphic occurrence. Grape Creek Formation, Leonard Series, Lower Permian.

Age. Early Permian, Leonardian, Artinskian, Cisuralian.

Geographic occurrence. Miller Creek (USNM localities 40009, 40010, 40011, 40075, 40076), Baylor County, Texas.

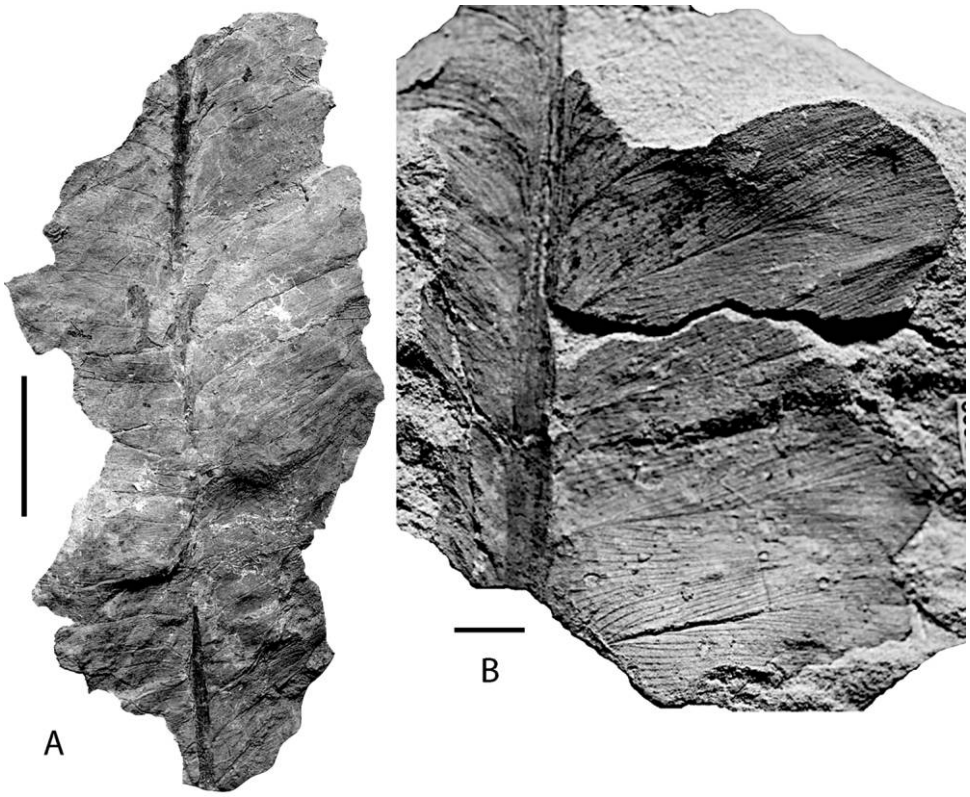

Fig. 4 *Comia greggii* n. sp., holotype and paratype. *A*, USNM 528611 from USNM locality 40076; scale bar = 5 cm. *B*, USNM 528609 from USNM locality 40076; scale bar = 1 cm.

Etymology. The specific name honors Donald R. Gregg of Seymour, Texas, whose assistance has materially advanced the study of fossil plants and animals in north-central Texas.

Description. This description is based on the holotype and paratype specimens, all incomplete, and all from the type locality in Baylor County, Texas. The material derives from poorly bedded tan sandstone exposed in the north-facing bluff along the banks of Miller Creek. This locality is in the Grape Creek Formation, which is a predominantly marine lateral equivalent to a portion of the Waggoner Ranch Formation (fig. 1).

All specimens are fragmentary single laminae exhibiting only secondary and tertiary veins. The largest specimen, the holotype (USNM 528611), is ~26 cm long and is broken at both ends, proportions suggesting that the pinna exceeded 30 cm in length (fig. 4*A*). Diminishing width at the distal portion of the specimen suggests that it is from near the apical area of the pinna. Its margins are shallowly crenate, with each lobe corresponding to the position of a secondary vein and its fascicle; the greatest distance from the point of origin of a secondary vein to the lobe tip is ~8 cm, so the total width of this pinna was at least 16 cm. Other specimens, based on half-widths of the lamina, would approximate total widths of 14 cm (USNM 528459) and 12 cm (USNM 528609).

The venation is open and three-ordered. The primary vein (fig. 4), which is not unusually stout, has a width of 8 mm through its incomplete length of 12 cm. The midrib surface is characterized by faint, parallel striations, with a prominent median rib that may represent the vascular system.

In a large fragment (USNM 528459) with only one side of the lamina preserved (fig. 5), remnants of the midrib extend across one edge of the specimen, and nine secondary veins arise at ~1.5 cm intervals. This spacing is usually equivalent to about one-third the length of the secondary vein. Similarly spaced, opposite–alternate pairs of secondary veins extend outward from the midrib (USNM 528609); in this specimen the tertiary veins are faint (fig. 4*B*). At their points of departure, the secondary veins are apically directed at a narrow angle for a short distance before bending outward toward the laminar margin; they then follow a nearly straight or only slightly bowed, broadly acute to nearly perpendicular, course toward the margin.

Tertiary veins arise immediately above the base of each secondary, in alternate or subopposite pairs (figs. 4–6). They depart at narrow angles (5°–10°) separated by 2–4 mm, and each tertiary typically dichotomizes twice between its base and its terminus at the laminar margin. The tertiary veins are thus close together (<2 mm apart) at their points of origin, and with each dichotomy become closer. In contrast, the width of the secondary vein diminishes until it reaches the same width as its tertiary derivatives. Each set of interfascicular tertiary veins consists of six to 10 veins that arise from the midvein between successive fascicles and dichotomize in a similar manner to the fascicular tertiary veins. This results in a crowded system of ultimate veins near the laminar margins; an exact count is not possible because of incomplete preservation, but there appear to be ~15 ultimate veins terminating in

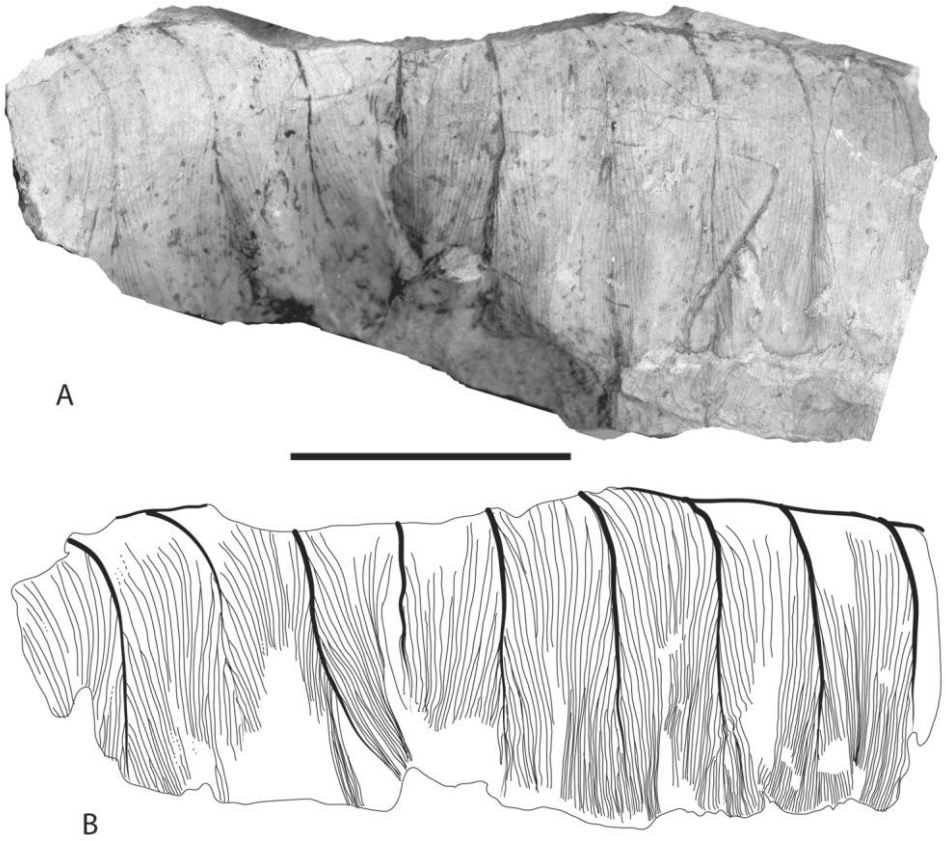

Fig. 5 *Comia greggii* n. sp., paratype USNM 528459 from USNM locality 40076; scale bar = 5 cm. *A*, Specimen exhibiting long secondary veins. *B*, Tracing of *A*.

a centimeter of laminar margin. Despite this dense arrangement of ultimate veins, there are no discernible anastomoses, and the venation appears to be completely open (fig. 5).

It is not known whether the leaf was a pinnate frond or a single lamina; both morphologies may have been present on the same plant, depending on the position of the leaf on the plant or the age of the plant at the time the leaf was produced. The growth habit of the overall plant is not known. Even though our material consists only of incomplete pinna fragments, and no details of frond architecture are available for comparisons with previously described species, the large dimensions and crowded venation readily distinguish this material and warrant its description as a new species. In at least one instance (fig. 7), a peltate structure is seen adpressed to the surface of part of a pinnule of *C. greggii*.

Comia craddockii *Mamay, Chaney & DiMichele sp. nov. (Figs. 8, 9)*

Specific diagnosis. Frond once pinnate, moderately large, monopodial; rachis striate, stout, basally to ~11 mm wide. Frond outline lanceolate, to ~40 cm long. Pinnae closely set, alternate to subopposite, inserted at spacing of ~15 mm in the proximal portion of the frond and up to 30 mm distally. Basal pinnae perpendicular to rachis, distal ones broadly acute (~50°). Pinnae 5.0–10.0 cm long (shortest at frond base, longest near middle of frond); greatest width ~2.5 cm. Pinna margins entire to shallowly crenate; bases cordate but with the basiscopic margins increasingly decurrent distally, producing a wedgelike terminal segment with a rounded tip.

Lateral venation compact, uniformly spaced. Secondary vein gently arching outward from stout midvein with ~3-mm basal width. Secondary veins alternate to subopposite, 4.0–7.0 mm apart, dividing once to rarely three times about middle of the lamina, such divisions producing several infrequently dichotomizing fascicular tertiary veins. One-to-three interfascicular tertiary veins arise from midrib and proceed undivided to margin. All fasciculate tertiary veins arise at narrow angles, resulting in densely compact vascular system with symmetry only slightly distorted by nearly obscure fascicular organization. No anastomoses or incomplete fascicular veins known; ~10–15 ultimate veins terminating in 1 cm of foliar margin.

Holotype. USNM 508138 (figs. 8, 9).

Type locality. Brushy Creek, USNM locality 38902.

Referred material. USNM 536416, USNM 536417, both from USNM locality 41377; USNM 536420 from USNM locality 40996; USNM 536421 from USNM locality 40643; USNM 41778 from USGS locality 8966.

Stratigraphic occurrences. Upper Waggoner Ranch Formation to middle Clear Fork Group (Leonardian) and equivalent strata.

Age. Early Permian, Leonardian, Artinskian, Cisuralian.

Geographic occurrences. Baylor, Taylor, Palo Pinto, and Knox counties, Texas, and Tillman County, Oklahoma. USNM locality

Fig. 6 *Comia greggii* n. sp., paratype USNM 530888 from USNM locality 40010; scale bar = 1 cm.

numbers 41019, 42292, 40008, 38904, 41008, 41377, 38902, 40048, 38907, 40994, and 40095. USGS locality number 8966.

Etymology. The specific name honors Kenneth Craddock of Denton, Texas, whose dedication to paleontology has helped numerous paleontologists find and recover the fossil fauna and flora of north-central Texas.

Description. This species is moderately abundant in the lower part of the Clear Fork Group and is known from only two localities in the middle Clear Fork.

Most specimens are fragments showing only a few pinnae, but one large specimen (figs. 8, 9) was recovered in both part and counterpart and appears to represent a nearly complete frond. This specimen, designated the holotype (USNM 508138), is 32 cm long, with apparently only a small portion of its apex and base missing; hence, its total length probably was ~40 cm. The pinnae are relatively long and narrow, with compact lateral venation, the homogeneity of which renders the comioid organization somewhat less conspicuous.

The holotype has a stout monopodial rachis with a basal width of 11 mm, bears 24 closely set, alternate to subopposite pinnae, 12 on either side (fig. 8). The pinnae arise at intervals of ~15 mm in the proximal region of the frond, increasing to nearly 30 mm distally.

The basal pinnae of the holotype (fig. 9) are perpendicular to the rachis, but the angles of attachment gradually decrease to ~50° near the frond apex. In some specimens the angle of attachment of distal pinnae is slightly more acute.

The pinnae range from ~5.0 to 10.0 cm in length. The greatest observed width was 2.5 cm. The shortest pinnae occur at the base and the longest at about the middle of the frond. Pinna margins are entire to shallowly crenate. The bases of the proximal pinnae are mostly cordate with equally rounded sides, but their basiscopic margins tend to become increasingly decurrent toward the distal portion of the frond, reaching nearly to the upper margin of the subjacent pinnae. Between the uppermost few pinnae the lamina becomes coalescent, forming a wedgelike terminal segment with a rounded tip.

The lateral venation of *C. craddockii* is compact and uniformly spaced, gently arching outward from a fairly stout midrib. Secondary veins are ~3.0 mm wide at the base. The secondary veins arise alternately or suboppositely, ~4.0–7.0 mm apart; these are most clearly distinguished in foliar areas where the lamina is slightly creased and vaulted. There, observed under oblique lighting, the secondary veins stand out as curved ridges delimiting the successive interfascicular areas (figs. 8, 9). Otherwise, the secondary veins are often difficult to distinguish except for their division, at about the midpoint of the lamina. There they undergo one to rarely three divisions that produce several fascicular tertiary veins, which dichotomize infrequently. One to three interfascicular tertiary veins arise between fascicles and rarely divide during their course to the margin. All the vein divisions create narrow angles, resulting in a compact system of veins with symmetry only slightly disturbed by the nearly obscure fascicular organization. No anastomoses or incomplete veins have been observed. Approximately 10–15 ultimate veins terminate at the foliar margin.

Comparison. In its overall physical appearance the frond of *C. craddockii* rather resembles the penultimate division of a bipinnate neuropterid frond, so our reference to the ultimate segments of *C. craddockii* as "pinnae" rather than "pinnules" could be challenged by the discovery of more complete specimens demonstrating an additional degree of pinnation. However, the clearly comioid ultimate venation of the Texas material supports the present terminology in the absence of additional information relative to the gross architecture. This species is readily distinguishable from the other North American comioids by its relatively long and narrow pinnae and its compact lateral venation, the homogeneity of which renders the fascicular organization considerably less conspicuous than in *C. greggii* or *Auritifolia* (Chaney et al. 2009). As stated above, the frond architecture of *C. greggii* is not known. However, should it be shown that the frond structure of *C. greggii* is once pinnate, a frond of that form would be large indeed, dwarfing the frond of *C. craddockii*. In its straight rachis, *C. craddockii* differs importantly from *Auritifolia* (Chaney et al. 2009), in which

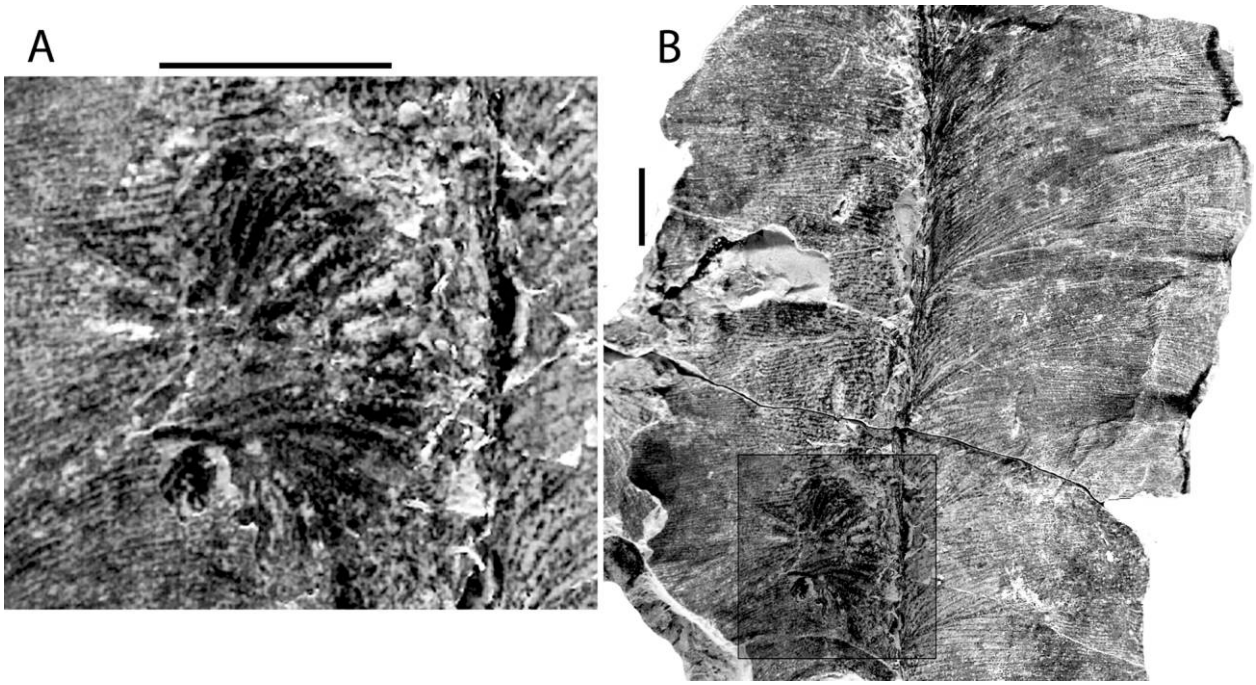

Fig. 7 *Comia greggii* n. sp., paratype USNM 530887 from USNM locality 40010, with peltate reproductive structure cf. *Sandrewia* adpressed to lamina but not biologically in direct connection; scale bars = 1 cm. *A*, Enlargement of peltate structure. *B*, Lamina with peltate structure adpressed.

the rachis divides terminally by unequal dichotomy to produce a characteristic pair of elongate terminal pinnae.

Comia *sp. (Fig. 10)*

Referred material. USNM 530889.

Stratigraphic occurrence. Waggoner Ranch Formation (Leonardian), Lower Permian.

Age. Early Permian, Leonardian, Artinskian, Cisuralian.

Geographic occurrence. Baylor County, USNM locality 40042.

Description. This incomplete specimen is missing the apical region. The leaf is not compound but has a distinct petiole and comioid venation. The secondary veins sweep out to the margin of the lamina broadly and gently. The pinna lamina has a lobate margin, with the secondary veins and fascicular bundles terminating in the lobes.

Discussion. The specimen is most similar to *C. greggii* in being noncompound, having a wide lamina and apparently entire margin. The sweep of the secondary veins is distinct from that of *C. greggii*, in which the secondary veins depart

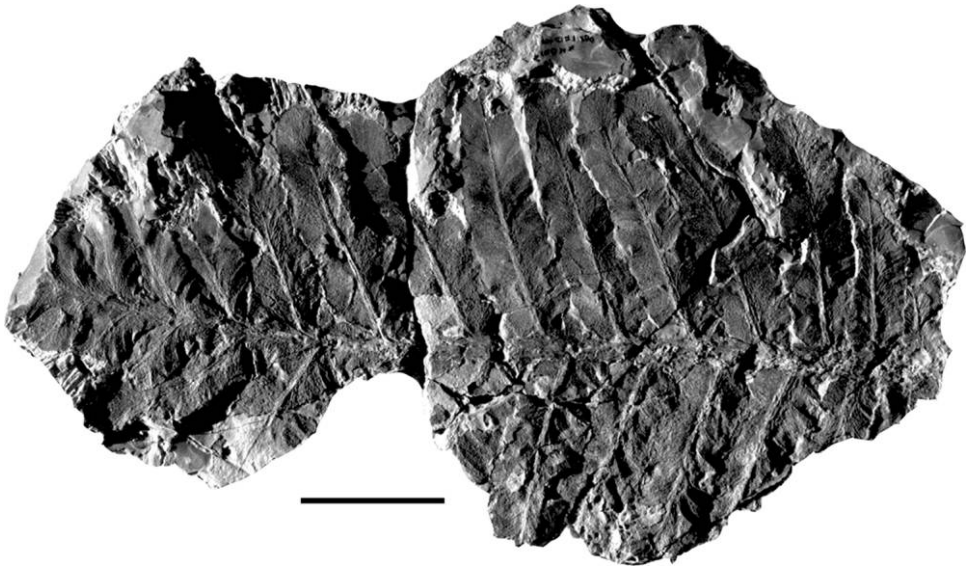

Fig. 8 *Comia craddockii* n. sp., holotype USNM 508138 from USNM locality 38902; scale bar = 5 cm.

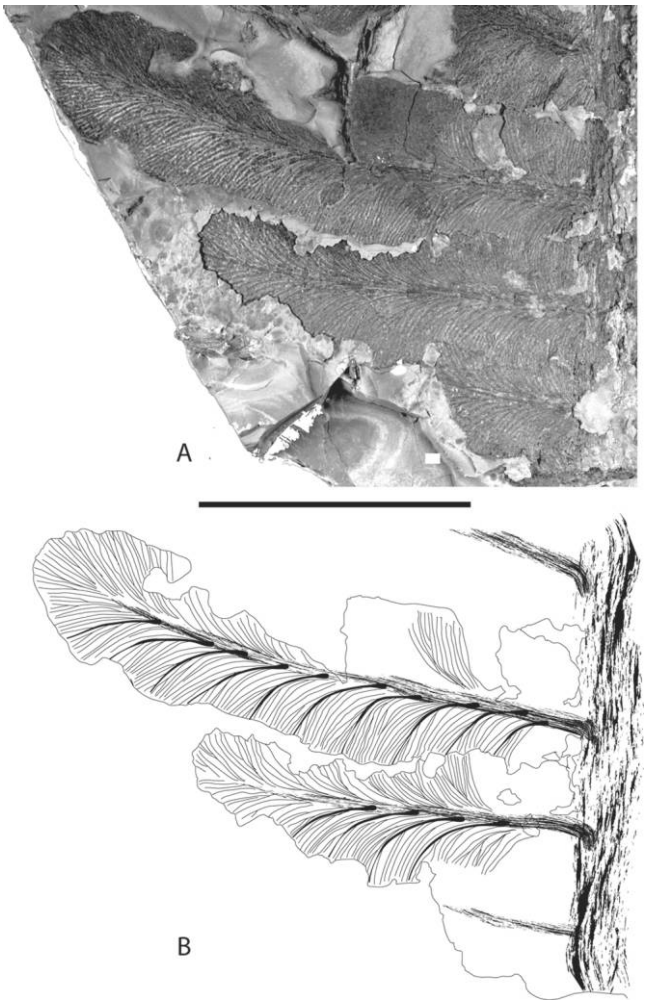

Fig. 9 *Comia craddockii* n. sp., holotype USNM 508138 from USNM locality 38902, enlargement of portion of counterpart to illustrate venation; scale bar = 5 cm. *A*, Lower left side near base of frond. *B*, Line drawing of same.

at nearly right angles to the primary vein. This complex of characters suggests that this specimen does not fit into either of the two new *Comia* species described herein. Despite being represented by a single fragment, this specimen is distinct enough to warrant documentation.

Comia *cf.* C. greggii *(Fig. 11)*

Referred material. USNM 530890.

Stratigraphic occurrence. Petrolia Formation (Leonardian), Lower Permian.

Age. Early Permian, Leonardian, Artinskian, Cisuralian.

Geographic occurrence. Baylor County, USNM locality 40022.

This small laminar fragment has venation similar to *C. greggii*. The margin is lobed. Secondary veins depart the midvein at approximately right angles. The fascicles end in the lobes and the interfascicular veins terminate in the sinuses. The specimen is tentatively identified as *C. greggii* because of these similarities, although it is significantly smaller than the few known *C. greggii* specimens. This is the oldest comioid known from north-central Texas.

Discussion

The comioid material reported has not been found in attachment to reproductive organs; hence, placement in the taxonomic hierarchy is difficult. It is not uncommon, however, to find both comioids and peltate reproductive structures in the same beds. Although not proof of identity, such consistent patterns of co-occurrence and the similarity to callipterid venation are supportive of a possible assignment to the seed fern order Peltaspermales.

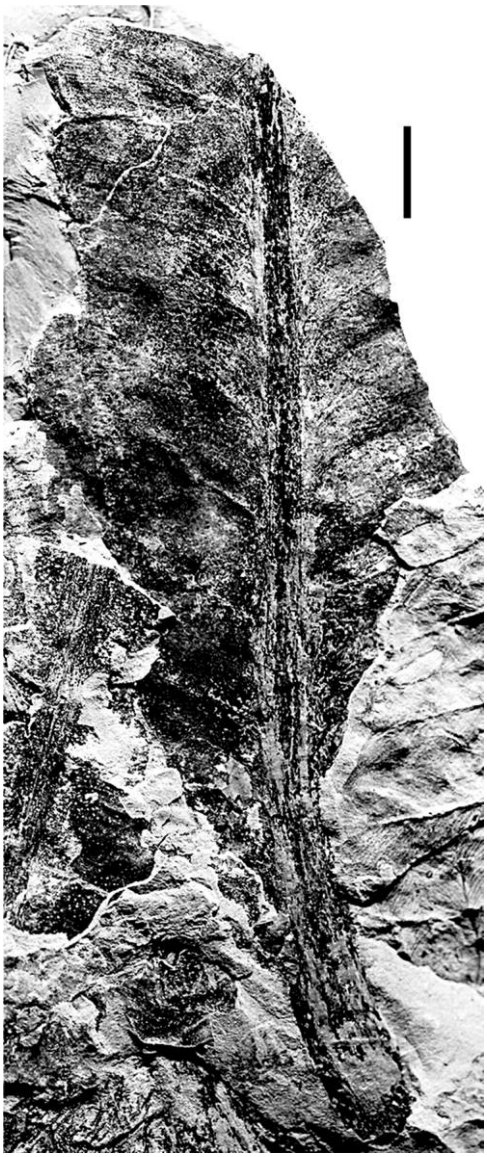

Fig. 10 *Comia* sp. USNM 530889 from USNM locality 40042; scale bar = 1 cm. Base of a leaf with the petiole attached. Surrounding matrix was digitally lightened a small amount to more clearly define the specimen.

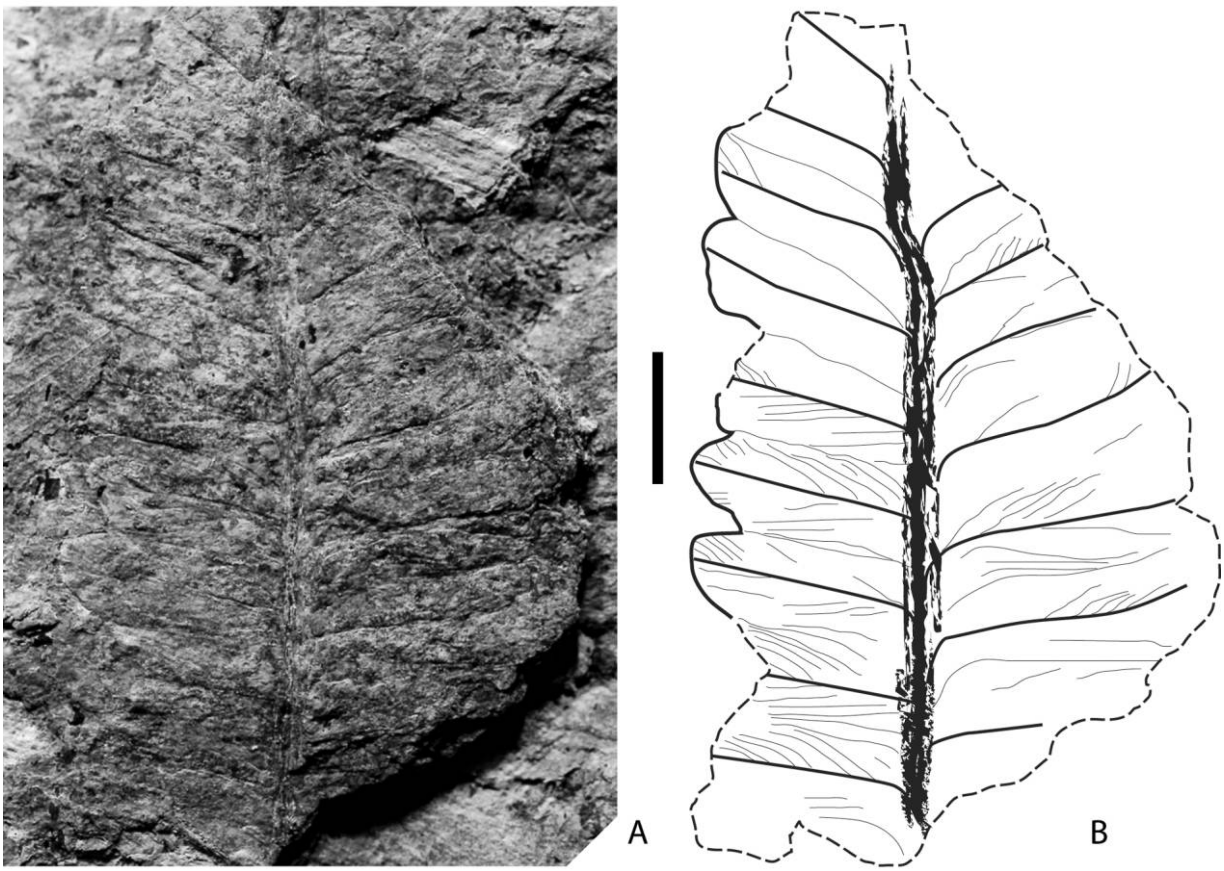

Fig. 11 *Comia* cf. *Comia greggii*, oldest known comioid, USNM 530890 from USNM locality 40022; scale bar = 1 cm. *A*, Small laminar fragment with comioid venation, secondary veins terminating in the lobes and interfascicular tertiary veins terminating at the margin in the sinuses. *B*, Line drawing of same. Specimen is preserved in sandy silt matrix. Organic debris makes the specimen difficult to interpret.

As indicated in appendix A, some 30 species of *Comia* have been named before this report. Along with the occurrence in the Matzitzi Formation in the state of Puebla, Mexico (Weber 2007), the Texas specimens represent the only known occidental occurrence of this group. All previous reports of comioids are based on material collected from Upper Permian strata of Eurasia (app. A) or the Middle East (Berthelin 2002).

The new *Comia* species from north-central Texas have the venation pattern diagnostic of all other *Comia* species (figs. 2, 3). The larger size and delicate venation of *Comia greggii* differentiate it from *Comia craddockii*. The two *Comia* species described herein are differentiated from *Auritifolia* (Chaney et al. 2009) by the lack of the pronounced anastomoses and blind endings that are characteristic of *Auritifolia waggoneri* (fig. 3).

At present, specimens unquestionably assignable to either *C. greggii* or *C. craddockii* are not known to overlap stratigraphically (fig. 1), nor are they known to co-occur. *Comia craddockii* and *A. waggoneri* do overlap stratigraphically but rarely co-occur, and then not in equal proportions at any of the sites collected to date.

In Texas the oldest representative of the comioids is here referred to *Comia* cf. *C. greggii* (early Leonardian USNM locality 40022) at the base of the Petrolia Formation. The associated flora from this locality indicates much wetter conditions (marattialean tree ferns dominate the assemblage) than for any of the later occurrences of the comioids. *Comia greggii* occurs at one locality, in the early Leonardian Grape Creek Formation (lateral equivalent of the Waggoner Ranch Formation). The lowest occurrence of *C. craddockii* is in the Lueders Formation, a near-shore, coastal-plain deposit that immediately overlies the rocks in which *C. greggii* occurs. *Comia craddockii* is the dominant form in the lower Clear Fork Formation but extends into the middle part, in small channel and floodplain lake deposits. There it co-occurs, as a rare element, with *A. waggoneri* high in the middle part of the Clear Fork Formation. *Auritifolia waggoneri* pinnules occur in the middle part of the Clear Fork Formation, not only as the predominant comioid but also as a dominant element of the flora as a whole. The middle Clear Fork Formation, deposited under similar conditions as the lower part of the formation, consists primarily of alluvial-plain channel deposits.

It is possible that the difference in stratigraphic occurrence among these comioids reflects subtle changes in environmental conditions. A systematic change in depositional conditions is not clearly evident. However, there are changes in the composition and dominance-diversity structure of the assemblages in which these different forms occur. Paleosol evidence (Tabor and Montañez 2002) indicates a drying trend through

the Clear Fork. The upper Clear Fork, from which plant fossils are not known, is a complex of weakly developed paleosols and thin beds of evaporites, probably formed in a coastal-plain setting.

The evolutionary relationship of the comioids must remain indeterminate until evidence of their reproductive biology can be established more firmly. Occasional co-occurrence with *Sandrewia/Autunia* type fructifications, typical of peltasperms (Kerp 1982), leads us to suggest peltaspermalean affinity (DiMichele et al. 2005). However, this must be considered only as an informed inference at our present state of knowledge. If peltaspermalean, these new taxa contribute to a growing awareness of the importance of peltasperms in both tropical and north temperate ecosystems during the Permian (Kerp and Haubold 1988; Naugolnykh and Kerp 1996; Naugolnykh 1999; Kerp 2000), a time when this group may have been undergoing a rapid and morphologically wide-ranging evolutionary radiation.

At the present time, the North American comioids, having no recognizable predecessors, are reasonably interpretable as corroborative evidence of plant migration between North America and Asia, with North America as the likely point of origin (Mamay 1960).

Acknowledgments

This work could not have been accomplished without years of cooperation from the residents of north-central Texas. Notable among these are Don Gregg and the late Dr. Dan Jackson, of Seymour. Many landowners and ranch managers have, over the past 40 years (S. H. Mamay [USGS], then to W. A. DiMichele and D. S. Chaney [NMNH]), provided access and other assistance that made this work possible. The restricted stratigraphic range of the comioids and the distribution of outcrops of appropriate strata made it possible to thank the following landowners and managers: A. B. Wharton and G. Willingham of the W. T. Waggoner Estate, Vernon; Pat Cowan, Wichita Falls; and the late Mr. and Mrs. Rufus Whittley and the late Mrs. Jet Russell, Seymour. We were assisted in the field by individuals who aided in collecting specimens and in geological investigations: Vincent Lyles, Pete Kroehler, and Steve Jabo, (NMNH); John Nelson, Illinois State Geological Survey; Kenneth Craddock and the late Louis Todd of Denton; and Robert Hook, Austin. We thank Isabel van Waveren, Naturalis, Leiden, for comments on an earlier draft. We thank Dr. E. Bugdaeva of the Far East Branch of the Russian Academy of Sciences, Vladivostok, and Dr. S. Naugolnykh of the Russian Academy of Sciences, Moscow, for the Russian abstract. Dr. Wang Jun, Academia Sinica, Nanjing, kindly provided the Chinese abstract. For translation of parts of the Chinese literature we thank Professors Wang Jun and Yao Zhaogi (retired) of Academia Sinica and Dr. Li Chengsen and Dr. Wang Shijun of the Chinese Academy of Sciences, Beijing. Assistance with the Russian literature was kindly provided by A. Kopylova, Novosibirsk State University and P. Wilf, Pennsylvania State University, University Park. Without the assistance of all these individuals, our access to important information would not have been possible, and we are grateful to all of them. The manuscript was reviewed by an anonymous reviewer and Michael Krings, Bayerische Staatssammlung für Paläontologie und Geologie und GeoBio-Cen, Munich. We appreciate the thorough and helpful reviews.

Appendix A

Chronological, Briefly Annotated List of Published Names of *Comia* spp. (Manuscript Names and Subspecific Names Omitted)

Comia pereborensis Zalessky 1934. Upper Permian, Pechora Basin. Neuburg 1961; Schwedov 1961; Rasskazova 1963; Gorelova 1969; Fefilova 1973; Burago 1983.

C. primitiva Neuburg 1948. Upper Permian, Kuznets Basin. Rasskazova 1963; Burago 1983.

C. dentata Radchenko 1956. Upper Permian, Kuznets Basin. Radchenko 1956; Rasskazova 1963; Nemejc 1968; Gorelova 1969; Fefilova 1973; Burago 1983.

C. osinowskiensis (Chaklov) Radchenko emend., 1956. Upper Permian, Kuznetz Basin. Chachlov 1931 as *Gigantopteris osinowskiensis*, Neuburg 1961; Rasskazova 1963.

C. dobrolubovae Tschalyschev 1960. Upper Permian, Pechora Basin. Rasskazova 1963; Fefilova 1973; Burago 1983.

C. latifolia Tschalyschev 1960. Upper Permian, Pechora Basin. Rasskazova 1963; Fefilova 1973; Burago 1983.

C. enisejevensis Schwedov 1960. Upper Permian, Pechora Basin. Neuburg 1961; Schwedov 1961; Rasskazova 1963; Gorelova 1969; Fefilova 1973; Durante 1976; Burago 1983.

C. major Schwedov 1961. Upper Permian, N. Yeniseyck Region. Rasskazova 1963; Huang 1977.

C. lata (Neub.) Neuburg 1961 (=*Callipteris*?). Upper Permian, Kuznets Basin. Neuburg 1961; Rasskazova 1963.

C. saurica Mikunov 1962. Upper Permian, Kenderlyk Trough (E. Kazakhstan). Rasskazova 1963.

C. dentifolia Rasskazova 1963. Upper Permian, Norilsk Region.

C. laceratifolia (Halle) Rasskazova 1963. (=*Odontopteris* [?*Callipteris*] *laceratifolia* Halle 1927.) Upper Permian, China. Rasskazova 1963.

C. norilskiensis Rasskazova 1963. Upper Permian, Tunguska Basin. Fefilova 1973.

C. yichunensis Huang 1966. Upper Permian, NE China. Li et al. 1974; Huang 1977; Burago 1983.

C. arctica Gorelova 1969. Upper Permian, Norilsk Region.

C. sp. Mogucheva 1973; reported from the Early Triassic, Tunguska Basin, but the genus is not recognizable in the illustration.

C. maganakovkiensis Sukhov 1962. Upper Permian, Kuznets Basin. Rasskazova 1963; Gorelova et al. 1973.

C. microphylla Huang 1977. Upper Permian, NE China.

C. multinervis Huang 1977. Upper Permian, NE China.

C. obese Huang 1977. Upper Permian, NE China.

C. shenshuensis Huang 1977. Upper Permian, NE China.
C. tenueaxis Huang 1977. Upper Permian, NE China.
C. cangfanggouensis Hu 1980. Upper Permian, NW China.
C. xingjiangensis Gu (in Dou Yawei et al. 1983). Upper Permian, NW China (emend Liu and Yao 1996).
C. kugaensis Wu 1985. Upper Permian, NW China.
C. tarimuensis Wu 1985. Upper Permian, NW China.
C. partita Zhou and Zhou 1986. Upper Permian, NW China.
C. congermana (Zalessky) Burago 1983. Upper Permian, Prymorye Region, SSSR.
C. latiloba Burago 1983. Upper Permian, Prymorye Region, SSSR.
C. contracta Liu and Yao 1996. Upper Permian, NW China.
C. minor Liu and Yao 1996. Upper Permian, NW China.
Comia sp. general term not referring to any one author's concept. Durante 1976; Liu and Yao 1996.

Appendix B

Localities from Which Different Comioids Have Been Recovered, Grouped in Isosedimentological Categories (in Each Group, Localities Listed from Youngest to Oldest)

Active channel accumulations:
  Fine sandstone and siltstone deposits, trough cross-bedded, indicative of bars. Plant fossils occur in foreset troughs.
    USNM locality 38908., lower Clear Fork Group.
    USNM localities 40659, 40989, 40990, 40991; middle Clear Fork Group.
    USNM locality 40982; middle Clear Fork Group.
    USNM locality 40980; middle Clear Fork Group.
    USNM localities 40656, 40657, 40979, 40993; middle Clear Fork Group.
    USNM localities 40973, 40651, 40652, 40974; middle Clear Fork Group.
    USNM localities 40977, 40987, 40988, 40992; middle Clear Fork Group.
    USNM localities 40009, 40010, 40011, 40075, 40076 and USGS 10167; Grape Creek Formation.
    USNM localities 40022, 40023, 40683; Petrolia Formation.
Floodplain deposits:
  Finely laminated clay deposits with abandoned channel areal and/or cross-sectional geometries:
    USNM localities 41005, 41006, 41007, 42292; middle Clear Fork Group.
    USNM locality 40972; middle Clear Fork Group.
    USNM localities 38907, 40045, 40046, 40047, 40643, 41001; lower Clear Fork Group.
    USNM localities 38901, 38902, 40048; lower Clear Fork Group.
    USNM locality 40048; lower Clear Fork Group.
  Clay and siltstone deposits of indeterminate areal or cross-sectional geometry with tabular to laminar bedding:
    USGS locality 8966; Vale Formation.
    USNM locality 40984; middle Clear Fork Group.
    USNM locality 40985; middle Clear Fork Group.
    USNM locality 40649; middle Clear Fork Group.
    USNM localities 40995, 40996, 40997; lower Clear Fork Group.
    USNM locality 40994; lower Clear Fork Group.
    USNM locality 41010; lower Clear Fork Group.
    USNM localities 38904, 38905, 38906, 40597, 40598, 40599; lower Clear Fork Group.
    USNM locality 40041 and USGS locality 10055; Lueders Formation.
    USNM localities 40039, 40040, 40042, 40043, 40689; Waggoner Ranch Formation.
    USNM locality 41015; Garber Formation.

Appendix C

Table C1

Comparison of *Comia greggii* n. sp., *Comia craddockii* n. sp., *Auritifolia waggoneri*, and Other *Comia* spp.

	Frond			Pinnule							Vein				
	Size (mm)	Char. of top	Rachis thickness (mm)	Pinnule/ rachis angle	Apex form	Base char.	Length (mm)	Width (mm)	Pinnule margin char.	Pinnule form	No. fascicular	No. interfascicular	Midrib thickness (mm)	No. tertiary per cm of margin	Phylotaxy, arrangement density
A. waggoneri Chaney et al. 2009	Variable; 120 L × 80 W; 620 L × 310 W	Overtopped	30	Upper 35°; lower 90°	Rounded	Decurrent	11–>400	8–110	Straight to deeply lobed	Elongate	5–10	2–10	3–4, to 8	10–15	Obovate
C. greggii (sp. nov.)	Unknown	Unknown	Unknown	Unknown	Unknown	Unknown	200–300	160	Shallowly crenate	Unknown	20–25	6–10	8	15	Unknown
C. craddockii (sp. nov.)	Length 470; greatest width 200	Simple pinnate	11	Upper 50°; lower 90°	Rounded	Cordate to decurrent	50–120	25	Entire to shallowly crenate	Elongate	5–8	1–3	1.5	10–15	Alternate to subopposite
C. pereborensis Zalessky 1934	Unknown	Simple pinnate	Unknown	Upper 45°; lower 80°	Acute	Slightly restricted or decurrent	70	22	Slightly wavy to crenate	Elongate-lanceolate	Unknown	1–2	1.5	22–24	Subopposite at base; alternate distally
C. (?) *primativa* Neuburg 1948	Unknown	Unknown	Unknown	Unknown	Unknown	Unknown	Unknown	25	Smooth	Unknown	Unknown	1	Unknown	20	Unknown
C. dentata Radchenko 1955	Unknown	Unknown	2.5	Unknown	Unknown	Abruptly terminated, not decurrent	50–85	20–35	Deeply incised, ovate-triangular lobes	Linear-lanceolate	4–7	1–2	Unknown	Unknown	Alternate
C. osinowskiensis (Chachlov) Radchenko 1955	Unknown	Simple pinnate	5	Unknown	Ovate-rounded, somewhat acute	Abruptly rounded	25–100	11–25	Slightly wavy	Triangular-lanceolate	4–8	1	Unknown	Unknown	Unknown
C. enisejevensis Schwedov 1960	Width 70	Simple pinnate	4.5	Upper 60°; lower 90°	Unknown	Forming limbus	150	70	Crenate	Unknown	Unknown	Unknown	.5–.7	50	Unknown
C. dobrolubovae Tschalyschev 1960	Unknown	Simple pinnate	11	60°–70°	Rounded	Strongly decurrent	120	30	Deeply incised to oblique lobes	Linear-lanceolate	Unknown	5–7	Unknown	20–26	Opposite to subopposite
C. latifolia Tschalyschev 1960	Irregularly elongate, rhomboid	Simple pinnate	Unknown	Upper 40°–45°; lower 90°	Rounded	Unknown	70–145	21–64	Deeply incised to narrow tongue-shaped lobes	Linear-lanceolate	Unknown	2–3	Unknown	24–26	Alternate
C. enisejevensis Schwedov forma *petschorensis* Tschalyschev 1960	Width 300; oblong, irregular rhomboid	Simple pinnate	15	Upper 45°; lower 90°	Rounded	Forming limbus	15–140	10–25	Slightly incised, rounded lobes	Linear	12–15	2–3	.25–1.75	24–30	Opposite
C. major Schwedov 1961	Larger; width >130–300	Unknown	Width 5–12	50°–90°	Obtusely pointed	Forming limbus	65–130	27–40	Entire or serrate	Long deltoid to lingulate	3–5	Probably only 1	1–1.2	14–18	Alternate; some rather congested
C. lata Neuburg 1961	Middle; width >112	Simple pinnate	Width of upper part 3	60°–70°	Acute	Slightly decurrent	47–58	20–22	Entire or slightly serrate	Lanceolate	Unknown	Unknown	Very slender; width <1	16–20	Probably opposite; lower part congested; upper part scattered
C. maganakovkiensis Sukhov 1962	Larger; width >140	Simple pinnate	Width 2.5	50°–90°	Acuminate	Forming limbus	87	25	Undulate and serrate	Linear to long deltoid	4–8	1–2	<1	16–24	Opposite scattered
C. saurica Mikunov 1962	Middle; width >100	Bipinnate	6	Upper 50°–60°; lower 70°–80°	Rounded	Slightly decurrent	21–54	13–24	Slightly undulate and crenate	Long lingulate	4–6	2–3	Slender	18–20	Alternate; arrangement slightly scattered

Table C1
(*Continued*)

	Frond			Pinnule							Vein				
	Size (mm)	Char. of top	Rachis thickness (mm)	Pinnule/ rachis angle	Apex form	Base char.	Length (mm)	Width (mm)	Pinnule margin char.	Pinnule form	No. fascicular	No. interfascicular	Midrib thickness (mm)	No. tertiary per cm of margin	Phylotaxy, arrangement density
C. dentifolia Rasskazova 1963	Unknown	Unknown	8–10	50°–60°	Unknown	Forming limbus	>150	35–40	Deeply incised lobes with acute tips	Linear	Unknown	4–5	2–3	16–28	Alternate
C. norilskiensis Rasskazova 1963	Width >100	Simple pinnate	3.4–4	50°–60°; sometimes up to 90°	Rounded	Forming limbus	45	22	Slightly crenate	Tongue shaped	7–9	4	Unknown	24–36	Alternate; subopposite; rarely opposite
C. yichunensis Huang 1966	Larger; width of middle and lower part ~400	Probably bipinnate	Width of middle and lower parts ~8–14	60°±	Acuminate	Decurrent	220	54	Undulate or serrate	Ensiform	7–9	4–7	4	22–26	Alternate to subopposite; lower part congested; upper narrow spaces
C. arctica Gorelova 1969	Width >170	Simple pinnate	6–7	Upper 40°–50°; lower 50°–70°	Pointed	Decurrent	120	30–35	Unknown	Linear to oblong, tongue shaped	Unknown	1–2	1.5–2	28	Subopposite
C. dentata Radchenko f. *multinervia* Fefilova 1973	Unknown	Simple pinnate	11	60°–70°	Unknown	Forming limbus	>148	>160	Incised oval roundish-sharp lobes	Linear-lanceolate	20	1–2	Unknown	12–16	Alternate
C. noriliskiensis Rasskazova f. *grandifolia* Fefilova 1973	Irregular; rhomboid	Simple pinnate	Unknown	Upper 60°; lower 90°	Rounded	Forming limbus	>86	>28	Wavy to slightly crenate	Linear-lanceolate	4–6	2–3	.5–2	24–26	Subopposite
C. tenueaxis Huang 1977	Large; width >140	Bipinnate	Width 2	40°–45°	Acuminate	Front side contracted, back side forming limbus	>100	30–35	Entire or slightly split	Ensiform	5–7	1–2	2	16–18	Lower part pinnule overlapping; upper part congested
C. microphylla Huang 1977	Large; width >240	Simple pinnate	Width 2–6	Upper 40°–45°; middle, lower 40°–45°	Acuminate to rounded	Forming limbus	16–23	3.3–12	Entire or slightly undulate	Linear to ensiform	3–4	1–2(?)	Base ~1	25–28	Alternate congested
C. obese Huang 1977	Larger; width >200	Unknown	Width 8	50°–90°	Rounded	Forming limbus	110	33	Entire	Ensiform	2–3 or 1–2 (upper part)	1	Base ~1.1	24–28	Opposite congested
C. shenshuensis Huang 1977	Middle; width >140	Unknown	Width 7	50°–90°	Rounded	Decurrent	59–86	15–26	Undulate	Linear, long lingulate	Max. 8, min. 2–3	2±	Base ~2.3	32–36; max. >40	Opposite scattered
C. multinervis Huang 1977	Larger; width >160	Unknown	8	60°–80°	Obtuse-rounded	Slightly decurrent	90	25–27	Entire or serrate-undulate	Long lingulate	4–5	1–2	Base ~1.1	32–36	Alternate, congested
C. canfanggouensis Hu 1980	Unknown	Unknown	Unknown	Unknown	Unknown	Unknown	Unknown	Unknown	Unknown	Unknown	Unknown	3–5	Unknown	35–40	Unknown
C. latiloba Burago 1983	Length 190; width 150	Unknown	3–12	40°–75°	Obtuse	Decurrent	98	35	Incised to smooth	Linear	Unknown	Unknown	Unknown	20–26	Subopposite
C. congermana (Zalessky) Burago 1983	Length >150; width 170	Simple pinnate	5	Top 40°–45°; bottom 70°–80°	Obtuse	Decurrent	80	16–24	Deeply incised	Lanceolate	Unknown	Unknown	Unknown	24–28	Unknown
C. kuqaensis Wu 1985	Width 180	Bipinnate	Unknown	Unknown	Unknown	Contracted	Unknown	Unknown	Incised-lobed	Unknown	8–12	2–3	Unknown	Unknown	Unknown
C. tarimensis Wu 1985	Width 140	Bipinnate	3–4	40°–50°	Unknown	Decurrent	Unknown	Unknown	Lobed	Lanceolate	10–14	1–2	Unknown	Unknown	Unknown
C. partita Zhou et Zhou 1986	Length >130; greatest width 100	Simple pinnate	4	60°–70°	Obtuse	Decurrent	60	20–30	Pinnatipartite to almost pinnatisect	Lanceolate to ensiform	20	1–2	1	30	Unknown
C. xinjiangensis Gu emend Liu et Yao 1996	Unknown	Simple pinnate	2	Unknown	Unknown	Decurrent	40	12–20	Lobed	Linear	8–12	1–2	Unknown	24–28	Alternate
C. contracta Liu et Yao 1996	Length >200; width 240	Simple pinnate	6–8	≈90°	Acuminate	Contracted	120	35	Serrate	Oblong-lanceolate	6–8	1	1.5	20–22	Subopposite
C. minor Liu et Yao 1996	Unknown	Simple pinnate	1	40°	Unknown	Decurrent	>30	10	Crenate-dentate to undulate	Elongate-deltoid	4–8	1	Unknown	24–28	Opposite

Note. The tables of Rasskazova (1963) and Huang (1977) were combined, and subsequently described species were added. The table has been modified to incorporate the vein terminology proposed in this article. Forms described in Russian, notably by Burago (1983) and Fefilova (1973), provide additional information about the earlier described taxa. Data in any individual cell may have been derived from several sources in additional to the original paper; such references are not indicated for each item but are cited in the Literature Cited. Number of veins per fascicle proved difficult to assess; number of veins per centimeter of pinnule margin is a better indicator of vein density. Char. = character.

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